GENETICS OF HYBRIDIZATION BETWEEN THE POCKET GOPHERS *THOMOMYS BOTTAE* AND *THOMOMYS TOWNSENDII* IN NORTHEASTERN CALIFORNIA

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Abstract.— Hybridization between the pocket gophers *Thomomys bottae* and *T. townsendii* at Gold Run Creek in Honey Lake Valley, Lassen County, California, is examined by electromorphic and morphologic characters and by the distribution of ectoparasitic mallophagan lice. Hybrid formation is minimal (about 12% of the total sample of 104 individuals examined), but both F$_1$ hybrids and a few presumptive backcross individuals are apparent. Nevertheless, no evidence of genic introgression based on five diagnostic allozyme loci is present in parental populations of either taxon within a mile of the hybrid zone. Similarly, louse species unique to each parental gopher host do not penetrate beyond the geographic limits of the genetic hybrid zone into the range of the opposite gopher species. A narrow zone of hybridization is thus concordantly defined by genetic, morphologic, and ectoparasitic parameters. These two gopher taxa are thus genetically if not reproductively isolated and should be considered separate biological species.

Thaeler (1968) was the first to record hybridization between the pocket gophers (*Thomomys bottae* and *Thomomys townsendii* in the Honey Lake Valley region of northeastern California. His study encompassed a multivariate morphometric assessment of cranial and pelage color characters, and he clearly demonstrated presumptive hybrid individuals based on morphological intermediacy. The possibility of limited gene exchange between the two species was thus raised. In his study, Thaeler compared the extent of hybridization between *bottae* and *townsendii* with that between intergrading subspecies of *T. bottae* in central California, using the differential extent of hybrid formation as a basis for making judgements as to specific status. Hall (1981), citing Thaeler's results, considered *townsendii* to be conspecific with *bottae* (but used the name *umbrinus*), based on his view (Hall 1943a,b, 1981:viii–ix) that any hybridization between taxa indicates a lack of reproductive isolation and thus conspecific populations.

In a series of reports examining the nature of genetic and reproductive interactions in a range of hybrid zones of the *Thomomys bottae* group of pocket gophers, we have attempted to draw the distinction between reproductive and genetic isolation between taxa, and have provided a set of operational criteria for defining species limits in situations of hybrid formation (see Patton et al. 1979, Patton 1981). We have argued that when hybrid formation is restricted to the F$_1$ generation, genetic isolation is complete even though reproductive isolation is not. From an evolutionary standpoint, the degree of genetic isolation is the significant component in any assessment of the systematic status of particular hybrid situations. Thus, the species *T. bottae* and *T. umbrinus* are genetically (and evolutionarily) separate units although they form occasional hybrids at one point of parapatric contact (Patton et al. 1972, Patton 1973). In contrast, the various morphologically, karyotypically, and/or genically differentiated units of *T. bottae* that have been examined at points of contact show wide ranges of backcross hybrid formation, with genic introgression extending beyond the limits of a morphologically and ecologically defined hybrid zone (e.g., Colorado River [Smith and Patton 1981]; White-Sacramento Mountains [Patton et al. 1979]; Rio Grande Valley [Smith et al. 1983]; Sangre de Cristo Mountains [Hafner et al. 1983]). Such evidence for genic introgression fully supports the view

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that these populations belong to but a single biological species. In these cases, neither reproductive nor genetic isolation is present.

Thaeler's (1968:548, Fig. 1) morphological analysis suggested a population composition of about 20–30% hybrid individuals at two areas of contact between *T. bottae* and *T. townsendii* in the Honey Lake Valley region in Lassen County, California: Gold Run Creek south of Susanville (between *T. b. saxatilis* and *T. t. relictus*) and Garnier Ranch to the southeast of Honey Lake (between *T. b. canus* and *T. townsendii relictus*). This estimate is considerably higher than the 11–15% hybrid proportion in the contact between *T. bottae* and *T. umbrinus* in Arizona (Patton 1973) but is substantially lower than that between fully intergrading subspecies of *T. bottae* (e.g., *T. b. pascalis* and *T. b. mewa* in central California, >76% [Thaeler 1968]; *T. b. actuosus* and *T. b. ruidosae* in south central New Mexico, >81% [Patton et al. 1979]). The extent of *bottae* x *townsendii* hybridization and Thaeler's (1968) recognition of possible backcross hybrid individuals suggests that genetic isolation may not be complete between these taxa. This raises the possibility that Hall's (1981) view regarding conspecificity of these forms may be correct.

We have approached this problem by combined genetic and morphological analyses of specimens from the contact zone of *bottae saxatilis* and *townsendii relictus* in Gold Run Creek. Genetic studies were limited to electromorphic analysis of protein variation; the morphological analysis incorporated a multivariate assessment of the placement of genetically known individuals to which could be compared the series originally examined by Thaeler, for which no genetic data are available. Additionally, an independent perspective of the geographic extent of potential introgression was obtained by examining the distribution of mallophagan lice on gopher specimens collected in the Gold Run Creek area. Parental populations of *townsendii* and *bottae* serve as hosts for *Geomydoecus idahoensis* and *G. shastensis*, respectively, both of which are included in the *oregonus* complex by Price and Hellenthal (1980). Previous investigations of *Geomydoecus* lice have shown them to exhibit a high degree of host specificity and to

- ● *T. b. saxatilis*
- ◐ *T. b. saxatilis* > *T. t. relictus*
- ◑ *T. b. saxatilis* X *T. t. relictus*
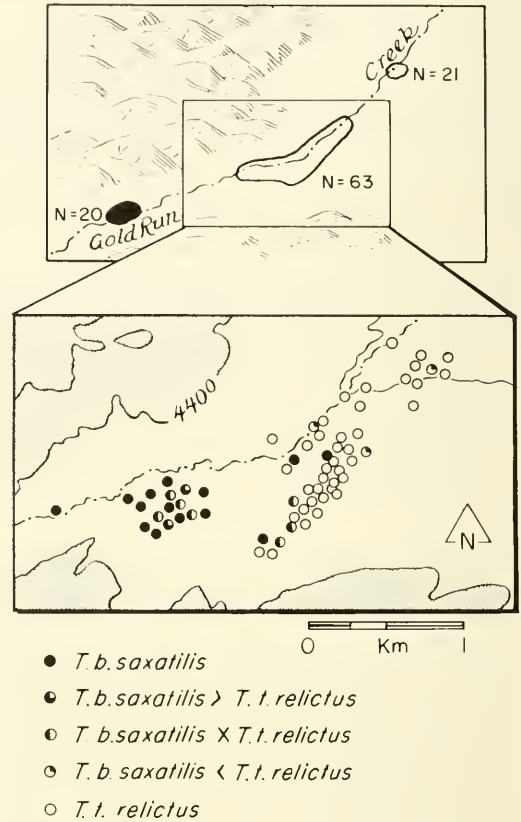- ◔ *T. b. saxatilis* < *T. t. relictus*
- ○ *T. t. relictus*

Fig. 1. Map of Gold Run Creek south of Susanville, Lassen County, California, showing location of parental *Thomomys bottae saxatilis* and *T. townsendii relictus* samples and hybrid zone. Inset: detailed map of hybrid zone showing trap localities of individual pocket gophers collected; genetic parents, F_1, and backcross hybrids are indicated.

support genetically based separations of gopher populations (Hellenthal and Price 1976).

MATERIALS AND METHODS

ELECTROPHORESIS.— 104 individuals from Gold Run Creek formed the basis for the majority of the analysis reported here. These include: (a) 20 specimens of presumptive *T. b. saxatilis* trapped at the head of Gold Run Creek, about 1.5 miles above the hybrid zone defined by Thaeler (1968); (b) 21 specimens of presumptive *T. t. relictus* trapped about 1 mile northeast of the mouth of Gold Run Creek; and (c) 63 individuals from within the hybrid zone along the lower reaches of Gold Run Creek (Fig. 1). Sample (a) was collected

during a single day in June 1981; samples (b) and (c) were collected over a five-day period in March 1982. Additional specimens of *townsendii* were available from the eastern end of Honey Lake Valley (Garnier Ranch [N = 14] and vicinity of Herlong [N = 44]) and from Standish (N = 18), about 14 miles to the east of Susanville. The additional specimens are from Patton and Yang (1977) and Rogers (1983).

Electrophoretic procedures followed those used in previous studies with *Thomomys* pocket gophers (e.g., Patton et al. 1972, Patton and Yang 1977, Smith and Patton 1981). Twenty-five presumptive loci were examined for population samples of *bottae saxatilis* and *townsendii* trapped away from the hybrid zone to identify those loci with alleles diagnostic to the two taxa (LDH-1 and -2, MDH-1 and -2, IDH-1 and -2, GOT-1 and -2, αGPD, IPO, Pept-1, SDH, 6PGD, PGM, PGI, ADH, Est-4, ADA, Ga3PDH, Alb, pre-Alb, Trf, MPI, Acon-1, and NP). Only those loci so diagnostic were examined for individuals trapped within the hybrid zone.

Morphometrics.— Morphological variation was examined for 14 cranial variables, as defined in previous studies (Patton et al. 1979, Smith and Patton 1984): occipito-nasal length (ONL), basilar length of Hensel (BaL), zygomatic breadth (ZB), mastoid breadth (MB), least interorbital constriction (IOC), rostral length (RL), nasal length (NL), rostral width (RW), diastema length (DL), maxillary tooth row length (MTRL), palatal width (PW), bullar length (BuL), rostral depth (RD), and incisive procumbancy (PRO). External dimensions were excluded because of the variance in the way individual investigators measure particular characters. Only specimens judged to be adult by criteria of the closure of the basisphenoid-basioccipital and exoccipital-supraoccipital sutures were utilized in the analysis.

Middorsal pelage color characteristics, including relative brightness (= value), excitation purity (= chroma), and dominant wavelength (= hue), were determined by use of a Bausch and Lomb Spectronic 505 recording spectrophotometer with a visible reflectance attachment. Only individuals in adult pelage were examined.

Males and females were treated separately in the analysis of cranial characters due to pronounced sexual dimorphism; both sexes were grouped for the colorimetric analyses.

The level of differentiation between the taxa in question and the possibility of individuals of morphological intermediacy were examined by the multivariate techniques of principal components and discriminant function analyses, using the program packages from MBS Consulting and SPSS (Nie et al. 1975), respectively, with the CDC 6400 computer at the University of California at Berkeley.

Host parasite association.— Lice were collected by brushing the gopher skin and were subsequently mounted on microslides and identified to species without prior knowledge of host identification or genetic information. Host parasite association and locality data obtained in this study were evaluated using a computerized taxonomic and geographic analysis system maintained on an IBM 370/168 computer at the University of Notre Dame (see Hellenthal and Price 1980). Mounted lice are deposited in the University of Minnesota insect collection.

Results and Discussion

Genic variation, hybrid formation, and introgression.— Samples of *T. b. saxatilis* from the head of Gold Run Creek (N = 20) differ by apparently fixed alleles at five loci when compared to those of *T. t. relictus* collected from Standish and the southeastern parts of Honey Lake Valley (combined N = 76): 6PGD, αGPD, NP, Acon-1, and pre-Alb. At an additional three loci (Trf, Est-4, and ADH), although the same dominant allele characterizes both taxa, secondary alleles were restricted to one or the other (Table 1). This set of loci can be used, therefore, as genetic markers to identify unequivocally F_1 as well as likely subsequent filial and backcross generation hybrids from the sample available from Gold Run Creek.

Genic hybrid index scores based on the genotypes of each individual for the five diagnostic loci are shown in Figure 2 (see Patton et al. 1979 and Smith and Patton 1981 for calculation of this index). When all individuals sampled from the Gold Run Creek

area are combined (N = 104), the majority (88.5%) have hybrid index scores indicative of either parental *bottae* or *townsendii*, and only 11.5% are grouped as genetic intermediates (hybrid indices of 0, +2, +4, etc.). Seven of these presumptive hybrids are exactly intermediate, suggesting that they are F_1 individuals; the remainder are heterozygous at one or more of the diagnostic loci and homozygous for one parental allele or the other at additional loci. Clearly, hybridization between *bottae* and *townsendii* along Gold Run Creek is minimal in amount and is largely limited to F_1 production. The proportion of hybrids in our genetic samples is lower than that suggested by Thaeler (1968) from his morphological analysis of this zone (20–30%). However, the pattern we observed is identical to that seen in the hybridization between *T. bottae* and *T. umbrinus* in southern Arizona, where F_1 males are sterile and F_1 females show greatly reduced fertility (Patton 1973). It contrasts markedly with cases of hybridization leading to extensive genic introgression in contact zones within *T. bottae* (see Patton et al. 1979, Smith et al. 1983, Hafner et al. 1983).

Hybridization at Gold Run Creek is not limited, however, to F_1 production, suggesting that F_1 individuals of either or both sexes

are at least partially fertile and that genetic isolation between the parental forms may not be complete. Nevertheless, no evidence of genic introgression extending beyond the immediate vicinity of the hybrid zone is available. No genetic characteristics of either parental form are seen in samples of the opposite taxon trapped at distances of about one mile from the location of hybrids in Gold Run Creek. This is true even though reproductive data indicate that hybrid individuals of both sexes have normal reproductive characteristics. Testis length, seminal vesicle length, and epididymal tubule diameter did not differ between hybrid males and those of either parent. Similarly, the only reproductively active adult female hybrid trapped contained five embryos of late term, a litter size characteristic of both species.

The reason for failure of genic introgression between the two taxa, therefore, is not at all understood. Clearly, available data do not suggest severe F_1 or backcross hybrid fertility or viability barriers, as is the case in *T. bottae* and *T. umbrinus* (Patton 1973). Limitation of introgression is, therefore, likely to be mediated by behavioral interactions determining both spatial territorial relationships and mating preferences. Spatially, the two taxa overlap only minimally

TABLE 1. Allele frequencies at eight diagnostic loci for samples of *T. bottae saxatilis* and *T. townsendii relictus* from Honey Lake Valley, Lassen County, California.

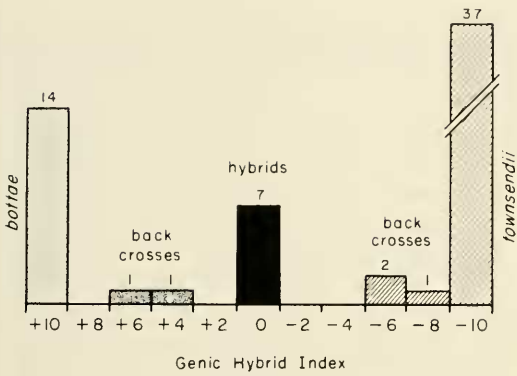| Locus | Allele | Saxatilis | Relictus | | |
		Upper Gold Run Creek (N = 20)	Mouth Gold Run Creek (N = 21)	Standish (N = 18)	Herlong/ Garnier Ranch (N = 44)
αGPD	119	1.00			
	100		1.00	1.00	1.00
NP	107	1.00			
	100		1.00	1.00	1.00
6PGD	100	1.00			
	88		1.00	1.00	1.00
Acon-1	117	1.00			
	100		1.00	1.00	1.00
preAlb	101	1.00			
	100		1.00	1.00	1.00
Trf	130	0.05			
	121	0.95	1.00	1.00	1.00
Est-4	102	0.175			
	95	0.825	1.00	1.00	1.00
ADH	–114	1.00	0.788	0.889	0.412
	–100		0.211	0.111	0.588

Fig. 2. Distribution of genic hybrid index scores for all specimens examined electromorphically from the hybrid zone along Gold Run Creek. Parental *bottae* and *townsendii* have +10 or –10 scores, respectively; F₁ hybrids are exactly intermediate with a score of 0; and those few specimens with scores between 0 and either +10 or –10 are considered genic backcrosses.

over but a few hundred meters (see Figure 1). Indeed, except for three *bottae* individuals, the two taxa were almost exclusive in their distributions along Gold Run Creek in 1982.

Morphological differentiation and hybrid intermediacy.— The morphological relationships of *bottae* and *townsendii* and their hybrids through the Gold Run Creek contact zone were examined from both colorimetric and cranial morphometric perspectives. In the former case, analysis was restricted to genically known individuals, and cranial character variation was assessed for the genetic samples as well as those collected in previous years, including the material examined by Thaeler in his 1968 study.

Variation for the three dorsal color variables measured is given in Table 2. The total sample was arranged into parental *townsendii* and *bottae*, genic F₁ hybrids, and presumptive backcross hybrids. The two taxa differ significantly (p < .01) in both dominant wavelength and brightness, but are inseparable in purity. This color difference is readily appreciated by the eye; *bottae saxatilis* is a rich cinnamon brown above and *townsendii relictus* is a pale yellow-gray. F₁ hybrids are intermediate between the parental forms in both wavelength and brightness, but are slightly skewed toward *bottae* (Fig. 2). The two backcross categories are appropriately intermediate between F₁s and their respective parental types. In general, hybrid class individuals are identifiable as such by eye from their color characteristics.

A principal components (PC) analysis was performed on the 14 cranial variables for all available samples of *townsendii*, *bottae*, and their presumptive hybrids from the Gold Run Creek area. This analysis was designed to determine the nature of differentiation between the taxa as well as to give insight into the morphological relationships of known and presumed hybrids to both parental forms. Only two components are necessary to explain more than 90% of the total variation in the samples (Table 3). Indeed, PCI alone accounts for 84% (males) to 89% (females), with all subsequent components contributing only weakly. All characters, except PRO, load positively and equally on PCI for both males and females. Such uniformity in loadings and the

Table 2. Mean, standard deviation, and range for the three colorimetric variables: dominant wavelength, purity, and brightness for *T. bottae saxatilis*, *T. townsendii relictus*, and their hybrids from Gold Run Creek, near Susanville, California.

Sample	N	Dominant wavelength	Purity	Brightness
Parental *townsendii*	46	582.1 ± 0.82 580–584	18.75 ± 2.42 15.00–23.44	12.81 ± 1.30 8.45–15.24
Backcross to *townsendii*	3	582.7 ± 0.58 582–583	17.52 ± 2.25 14.92–18.93	11.67 ± 0.90 10.86–12.63
F₁ hybrids	7	584.9 ± 1.21 583–586	21.68 ± 4.84 17.47–31.62	9.13 ± 0.73 8.35–10.52
Backcross to *bottae*	2	584.5 ± 0.71 584–585	14.32 ± 2.71 12.40–16.23	8.08 ± 0.08 8.02–8.14
Parental *bottae*	28	585.2 ± 2.03 583–594	17.55 ± 3.55 10.17–26.74	7.90 ± 1.32 5.36–11.57

high proportion of explained variance by PCI suggest that it is primarily a size axis, and that *townsendii* and *bottae* differ cranially predominantly by overall size in combination with differential incisor procumbancy; *bottae* with its small size has a more pronounced procumbancy (see character means, Table 3). There is apparently little marked shape change involved in the size differences in the skulls of *bottae saxatilis* and *townsendii relictus*, at least as identified by linear measurements.

The technique of step-wise discriminant function (DF) analysis was used to examine more closely the morphological relationship between the presumptive hybrids and both parental taxa. In this analysis, genetically known "pure" parental individuals of both taxa were used as a priori groups to which were compared individuals classed as hybrids by their respective genic index scores. In addition, specimens in the MVZ collections, including those examined by Thaeler in his 1968 study, were similarly compared to the parental reference series. This group included individuals identified morphologically as parental, "intermediate" hybrid, or hybrids closer to one or the other parental form (see Thaeler 1968:547).

The standardized discriminant functions for each variable are given in Table 3. Again, major discrimination is achieved by size

alone, with ONL loading most highly for both males and females. Since most of the remaining variables are highly correlated with ONL (r = .83 or higher in all cases, with the exception of PRO in both males and females), the high discriminating power of this variable reflects the overall size difference between *bottae saxatilis* and *townsendii relictus*.

Complete separation of the two genetically parental groups is apparent for both sexes in the DF analysis (Fig. 4). Those specimens identified by Thaeler previously as parental *bottae* or *townsendii* are grouped, with no exceptions, with their genetically known counterparts. Thus, the morphological distinctness of the two taxa is unambiguous. Genetic hybrids are generally intermediate between the parental forms in DF score. This is true for all F_1 hybrids of both sexes. Although the presumptive backcross individuals all show DF scores in the direction of the parental form involved in the backcrossing, some of these fall in the middle of the parental cluster and would not, therefore, be recognized as possible backcross individuals were it not for the electromorphic data. All specimens identified as possible hybrids by Thaeler are also intermediate in this analysis (Fig. 3).

DISTRIBUTION OF *Geomydoecus* LICE.— *Thomomys b. saxatilis* and *T. t. relictus* serve as hosts for the chewing lice *Geomydoecus*

TABLE 3. Character means for parental samples of *T. bottae saxatilis* and *T. townsendii relictus* from the Gold Run Creek region of Honey Lake Valley south of Susanville, California. Principal component (PC) and discriminant function (DF) loadings are given for each character.

| Variable	Character mean T. bottae		Character mean T. townsendii		PC 1		PC II		DF	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
ONL	40.21	36.62	48.44	44.79	.289	.280	.072	.084	−6.96	4.61
BaL	36.45	32.79	43.00	39.71	.285	.279	.141	.133	2.93	2.20
ZB	28.12	24.60	31.18	28.85	.270	.277	.286	.208	1.88	−2.59
MB	21.29	19.07	26.10	24.16	.285	.280	.017	.047	−3.53	1.99
IOC	6.43	6.46	7.03	7.11	.181	.247	−.626	−.098	−0.73	−0.27
RL	16.66	14.77	20.71	18.49	.270	.280	.127	.056	1.46	−1.71
NL	13.35	11.85	17.51	15.92	.285	.278	.071	.039	1.24	0.48
RW	7.80	6.65	9.92	9.04	.288	.278	.004	−.038	−0.65	2.10
DL	16.29	14.15	18.42	16.47	.264	.258	.316	.375	0.45	−1.80
MTRL	8.31	7.87	10.09	9.49	.270	.259	−.081	−.086	−0.34	1.44
PW	7.52	7.21	8.68	8.34	.275	.272	−.150	−.025	0.16	−0.71
BuL	7.18	6.95	8.37	8.03	.278	.266	.010	−.063	−0.58	−0.37
RD	7.20	6.38	8.59	7.80	.283	.276	.030	.006	−0.04	−0.36
PRO	4.24	3.98	2.61	2.56	−.198	−.201	.592	.873	−0.44	−0.45
			Eigenvalue		11.80	12.49	0.98	0.60		
			% contribution		84.28	89.19	7.01	4.29		
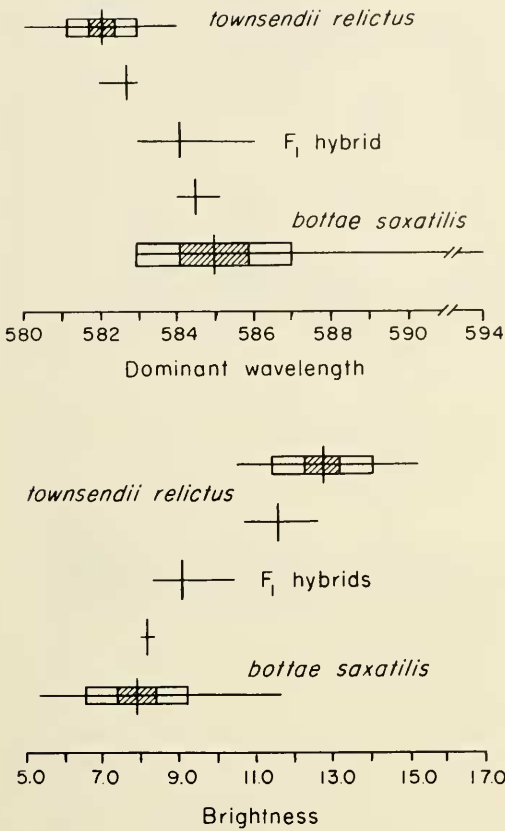
Fig. 3. Colorimetric relationships between *bottae* and *townsendii* and their hybrids from Gold Run Creek. Horizontal bar equals range; vertical bar sample mean; open box one standard deviation and hatched box twice the standard error of the mean.

shastensis and *G. idahoensis*, respectively. *Geomydoecus shastensis* has been collected from 12 subspecies of *T. bottae* representing 200 localities in northern California and southwestern Oregon. In only 5 of these localities were gophers found to also have another species of *Geomydoecus* louse. One of these was the *saxatilis-relictus* hybrid zone, and the remaining 4 involved 5 gophers with *G. angularis*. *Geomydoecus idahoensis* has been collected from 7 subspecies of *T. townsendii* representing 52 localities from northwestern California, southeastern Oregon, northern Nevada, and southern Idaho. In 4 of these localities, gophers were found to also have another *Geomydoecus* species, one of these being the *saxatilis-relictus* hybrid zone under consideration here. Two of the remaining localities were in the Garnier Ranch area

east of Honey Lake, where Thaeler (1968) conducted his study of the *T. b. canus* and *T. t. relictus* hybrid zone. Of the 10 gophers examined for lice from these localities and regarded by Thaeler as *canus-relictus* hybrids, 3 had only *G. shastensis*, 2 had only *G. centralis*, and 5 had both louse species. One additional locality in central Nevada also had one gopher with both of these louse species.

The distribution of louse taxa on pocket gophers through the *saxatilis-relictus* hybrid zone in Gold Run Creek thus serves as an independent view of the genetic and ecologic interactions of their hosts. Seventy-one of the genetically determined individuals were found to have lice, and the relationship between louse distribution and gopher taxon is given in Table 4. Three of 46 *relictus* specimens contained only *saxatilis* lice, and the remainder contained only *relictus* lice. All *saxatilis* trapped outside the hybrid zone had only *saxatilis* lice, and of the 13 individuals in the hybrid zone, 6 had only *saxatilis* lice and 7 had both species of lice. All *relictus* trapped outside the hybrid zone, except those from the *canus-relictus* contact to the east, had only *relictus* lice. The presumptive backcross individuals to *townsendii* had only the lice of that species; all other hybrid class individuals had either only *saxatilis* lice or both louse species. It is important that the geographic overlap of the distribution of the two louse species corresponded exactly with the middle of the hybrid zone, as defined by the genetic and morphologic characters of the gopher hosts. As with the electromorphic characters, there is no evidence of a louse species extending into the parental population of the opposite gopher host. The fact that some genetic "pure" gopher parental forms from the hybrid zone have the louse of the other gopher taxon is not unexpected. Lice are probably transferred among individuals by direct contact, which must occur if hybridization is to take place.

SYSTEMATIC AND EVOLUTIONARY CONCLUSIONS

Thomomys bottae and *T. townsendii* do hybridize where they meet along Gold Run Creek south of Susanville, California. The parental taxa differ by fixed alleles at five gen-
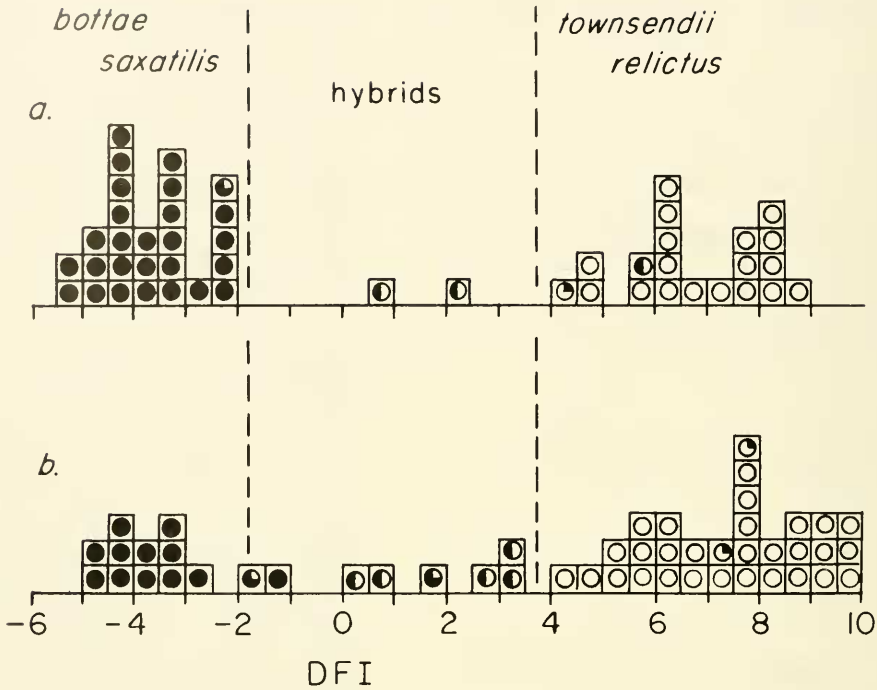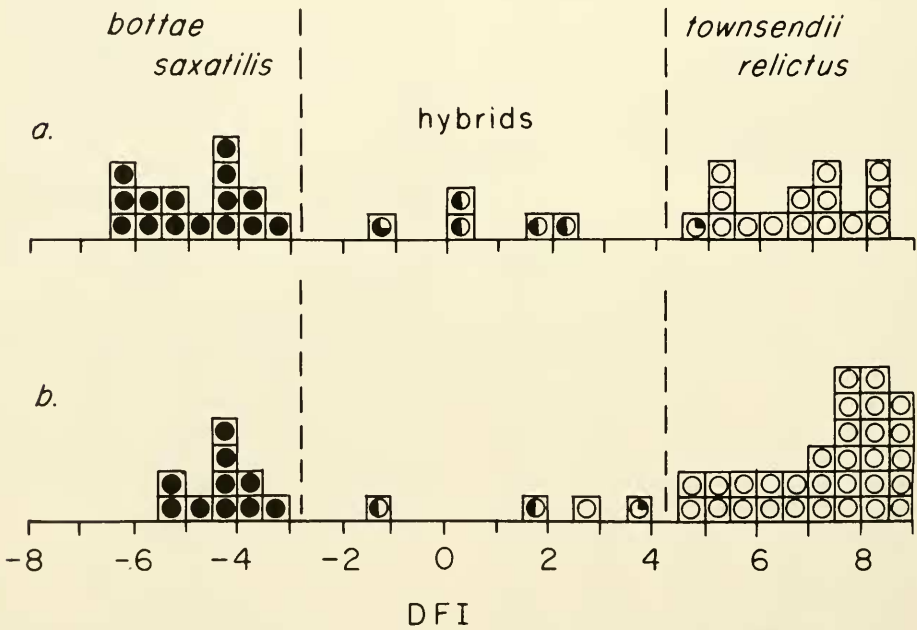
Fig. 4. Distribution of adult specimens from Gold Run Creek along the first discriminant axis for cranial characters. For both males and females, histogram *a* represents specimens for which no genic data are available, including those examined by Thaeler in 1968; *b* represents those specimens for which the hybrid or parental status is based on electromorphic characters (see text). Symbols in *a* indicate hybrids identified on morphological grounds by Thaeler (1968); those in *b* are based on genic data as in Fig. 1.

etic loci, facilitating the recognition of hybrid individuals and the extent of genic introgression. This hybridization is of limited scope; only 12 of 104 specimens (11.5%) examined electromorphically could be considered of hybrid origin. However, both F_1 and presumptive backcross hybrids were identified. If backcrossing occurs, then the F_1 hybrids must be at least partially fertile, and genic introgression between the parental forms is a possibility. In the present case, however, there is no evidence for introgression into parental populations of both taxa less than a mile distant from the hybrid zone. Although the hybrids appear reproductively competent, they must be at a decided disadvantage in competition for mates of either parent. Otherwise some genetic exchange between the two taxa would be expected.

F_1 hybrid individuals are intermediate in morphology, both cranially and in color characters; presumptive backcross individuals are skewed away from intermediacy in the direction of the parental form with which they share greater genetic similarity. This suggests that the genetic differences between the two taxa underlying the morphology are relatively simple and additive. Since so few intermediate individuals were found in samples collected at three intervals over a 25-year period (1960, 1969, and 1982), hybridization must be a sporadic event.

Importantly, genic, cranial, and color scores for any given hybrid are all concordant and intermediate, suggesting that hybridization is limited to the F_1 and but one or two subsequent filial or backcross gener-

ations. Repeated backcrossing would cause random assortment of these characters among a hybrid class of individuals, unless the controlling genetic elements were tightly linked. The latter is unlikely since the genome of both taxa consists of at least 38 linkage groups (i.e., the diploid number is 76 in both cases). Thus, the *bottae-townsendii* data contrast sharply with those from the *bottae actuosus* and *bottae ruidosae* hybrid zone in the White-Sacramento Mountains of New Mexico, for example, where two units likewise meet and hybridize along a narrow mountain canyon. In this case, hybridization is extensive because most individuals are various combinations of genetic backcrosses, with morphological and genic scores strongly discordant in many, indicating rather random reassortment of the parental characters.

The systematic and evolutionary significance of hybridization stems not from the lack of complete reproductive isolation between taxa, but rather in the presence of genetic isolation (Patton 1973, 1981; Patton et al. 1979). Since hybridization per se does not automatically produce actual gene exchange between the hybridizing forms, it is the degree of genetic rather than reproductive isolation that should be the measure of species status in hybrid situations. In the present case, *bottae* and *townsendii* are genetically isolated despite minimal hybridization over at least the past 25 years; there is simply no genic or morphologic evidence suggestive of introgression into either parental population, even at distances of a mile or less from the hybrid zone. Consequently, *bottae* and *townsendii* are evolutionarily separate units, and as such should be accorded full species status (contra Hall 1981).

TABLE 4. Distribution of *Geomydoecus* lice on pocket gopher host taxa through the contact zone between *Thomomys bottae saxatilis* and *Thomomys townsendii relictus* along Gold Run Creek. *T. bottae* is the host of *G. shastensis*, and *T. townsendii* is the host for *G. idahoensis*.

| Gopher: | Lice | | |
	G. idahoensis	*G. shastensis*	Both
T. townsendii	43	3	0
Backcross to			
T. townsendii	3	0	0
F_1 hybrid	0	3	4
Backcross to			
T. bottae	0	1	1
T. bottae	0	6	7

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